Behavior Associated with Pair Formation in the Banded Shrimp *Stenopus hispidus* (Olivier)[1, 2]

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ABSTRACT: Field observations of *Stenopus hispidus,* an incidental cleaning shrimp, indicate that it is normally found on the reef in male-female pairs. Pairs were taken to the laboratory, where they were separated and the individuals subsequently re-paired with equally sized "stranger" individuals of both the same and opposite sexes. Stranger shrimps of the same sex were highly aggressive and usually fought to the death. Among shrimp in aquaria there appeared to be no submissive or appeasement behavior. Stranger shrimps of the opposite sex tended to show initial fighting, followed by courtship and the formation of a breeding pair. Experiments were done to determine the major factors involved in mate recognition and hence pair formation. Pairs of shrimp allowed only chemical contact prior to being placed together showed quantitatively more fighting and more courtship than pairs allowed no sensory contact. Pairs of shrimp allowed only visual contact prior to being placed together showed quantitatively less courtship and equal fighting than pairs allowed no sensory contact. The supplement of controlled amounts of tactile contact to vision and olfaction resulted in quantitatively less fighting than occurred in control situations. Transfer to new surroundings seemed to increase the over-all level of aggression. The establishment of pairs and the behavior to other species of shrimps indicate that *Stenopus* is capable of species as well as individual recognition.

THE SHRIMP *Stenopus hispidus* (Olivier) has been reported from many parts of the Indo-Pacific region. It is characterized by long white antennae and antennules, by bright red bars banding its white body, and by enlarged, chelated, third pereiopods. *Stenopus* is common in Hawaiian waters, inhabiting rocky or coralline areas from a depth of a few centimeters to at least 30 meters. Field observations by C. K. Stolen, E. S. Reese, myself, and others indicate that the shrimp often is found in pairs, consisting of a male and a female of approximately equal size. Yaldwyn (1964 and 1966), however, reported an association between a large female and a comparatively tiny male found riding on her carapace.

Published descriptions of the ecology and ethology of *Stenopus* are few. Herrick (1891) gave a general description of the life history of *Stenopus.* Limbaugh, Pederson, and Chace (1961) described *Stenopus* as one of six shrimp species believed to enter into cleaning symbiosis with fish. C. K. Stolen (1964) described the ecology and general behavior patterns of *S. hispidus,* as well as some preliminary experiments with pair formation. Yaldwyn (1966) summarized the behavior patterns observed over a three month period in a captive pair of *Stenopus,* and outlined the relationships, systematic position, and fish-cleaning habits of the stenopodid shrimp. Finally, some aspects of the present study were reported by Johnson (1966).

The purpose of the present study is to investigate intraspecific sex recognition and pair formation of *Stenopus.* Questions asked include: How readily does *Stenopus* form pairs? Do pairs in the field always consist of a male and a female? How is intra-specific sex recognition accomplished?

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[1] Contribution No. 316 of the Hawaii Institute of Marine Biology, University of Hawaii, Honolulu. This study was done in the Department of Zoology of the University of Hawaii and at the Hawaii Institute of Marine Biology in partial fulfillment of the requirements for the Degree of Master of Science. Manuscript received February 9, 1968.

[2] The study was supported in part by Grants GB-1003 and GB-3651 from the National Science Foundation to Dr. Ernst S. Reese, and by the Eniwetok Marine Biological Laboratory.

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METHODS AND MATERIALS

Collection and Maintenance of Animals

Of the 78 shrimps studied in the laboratory, two-thirds were collected at night, by wading at low tide principally along the rock ledge of the Ala Wai Yacht Harbor, and occasionally on the Diamond Head or Ala Moana reefs (all on the island of Oahu). The shrimps were caught by using a dip net, a flashlight, and plastic collecting buckets. The remaining one-third were caught in the daytime by free diving with a dip net along the patch reefs of Kaneohe Bay in 1 to 3 meters of water. In both cases great care was required to prevent shrimps from losing appendages while struggling in the net. Those individuals which did lose appendages were immediately released. Each shrimp, or pair of shrimps, was taken to the laboratory in a separate collecting bucket.

The shrimps were kept in 16 eight-gallon, plastic, Aqua-Flaire aquaria with sub-sand filters. Before being placed in an aquarium, each shrimp was sexed and identified with a number. The criteria used for sex recognition were those given by Stolen (1964): (1) The pleopods of the female, when folded close to the body, extend anteriorly to the base of the second pereiopods. In males they extend only to the base of the fourth pereiopods. (2) A single, short, median spine is found on the ventral surface of each abdominal segment of the male. These spines do not occur in females, except those less than 3 cm in length. (3) At all times of the year most females carry a large mass of green eggs attached to the ventral side of the abdomen.

Normally two shrimps occupied each aquarium; those that were collected in the field singly, rather than as pairs, were separated from one another by various kinds of dividers, described below. The aquarium was filled with fresh, unfiltered sea water, and each half contained a small rock. The shrimps were fed a small piece of fish (*Chaetodon miliarias*) three times a week.

Test Procedure

Several hours were spent watching solitary and paired animals, to attain proficiency in recognizing and recording the fixed motor patterns described by Stolen (1964). The following test situation was then constructed.

Each aquarium was partitioned into two equal halves. A male and a female *Stenopus* from different pairs were placed on opposite sides of each partition. After both shrimps in an aquarium had molted once, the partition between them was removed and the interaction between the two animals was recorded. It was thought that the relative intensity and duration of fighting and courtship between shrimps, upon partition removal, would depend on the type, and/or degree of sensory contact allowed by the particular partition used. Thus, the sensory modalities involved in intra-specific sex recognition and pair formation could be determined. The following six experimental situations were used:

EXPERIMENTAL SITUATIONS I AND II (controls; no sensory contact prior to pairing): The original control situation (I) used no partitioning at all. Strange male and female shrimps were introduced simultaneously into the same unpartitioned aquarium, and observations were recorded immediately. In subsequent control situations (II), the shrimps were separated by a partition which allowed no sensory contact. Such partitions consisted of solid, opaque, plastic sheets sealed along the sides and bottom with Silastic Aquarium Sealant made by Dow Corning. Silastic provided a leak proof seal which could be loosened for partition removal. The tightness of the seal was ascertained by tinting the water on one side of each partition with a few drops of food coloring; in no case did coloring leak to the opposite side. Unequal water levels on opposite sides of the partitions further confirmed a tight seal. The originally clear plastic sheets were sprayed opaque using Seymour gloss white alkyd enamel paint.

EXPERIMENTAL SITUATION III (visual contact only): Partitions consisted of solid sheets of clear plastic, sealed along the sides and bottom with Silastic. Added food coloring and unequal water levels were again the tests of a tight seal.

EXPERIMENTAL SITUATION IV (olfactory contact only): Partitions consisted of opaque sheets of transite with seven small holes. The holes were 0.8 cm in diameter, spaced 3.2 cm apart, and made near the top of each partition to minimize the possibility of visual contact. Partitions were merely wedged in place, no sealing being necessary.

EXPERIMENTAL SITUATION V (visual and olfactory contact): Partitions consisted of clear sheets of plastic with 8 to 10 small holes. The holes were 1.3 cm in diameter, spaced at intervals of approximately 5 cm. Shrimps were never observed to insert appendages through the holes. Partitions were wedged in place.

EXPERIMENTAL SITUATION VI (visual, olfactory, and tactile contact): Partitions consisted of hard rubber sink mats of the kind used for draining dishes. The drain holes in the mats were enlarged to make extremely porous partitions, through which shrimps were often observed to touch appendages. Partitions were wedged in place.

In all experiments, the "partition interval" lasted until each animal had molted once (an average of 18 days), since a physiological cycle of the animal was deemed a better measure than a rigid time cycle. Also, it was theorized that molting might release chemicals important in sensory recognition. After partition removal, the shrimps were left together until the female had eggs (an average of 30 days). Breeding was used as the criterion for pair formation.

In all pair formation tests, the following control practices were followed: Shrimps which had been previously paired were not paired again. Solitary animals collected in the same area were never paired. Both animals in a given test were new to the particular aquarium. Aquaria were screened from one another by sheets of cardboard to eliminate inter-aquaria vision. Only shrimps with all appendages intact were used. If a shrimp lost an appendage during a test prior to partition removal, that particular test was terminated. An attempt was made to pair shrimps of the same size, and differences in carapace length never exceeded 1 cm.

Collection and Treatment of Data

Three times weekly each aquarium was checked for recent molts, and the animals were fed. An ethological analysis was made of the behavior patterns immediately following partition removal. During a ½-hour observation period divided into six five-minute intervals, the behavior of each shrimp, during each interval, was recorded. Each encounter between shrimps was classified as either an agonistic or courtship encounter. The number of agonistic and/or courtship encounters for each observation period was plotted against time. In addition, feeding, grooming, and walking behavior was recorded. No record was made of behavior duration.

The mean levels of courtship and/or agonistic behavior per each 5-minute interval of the respective pair formation experiments were statistically compared using t tests, treating the data as group comparisons of unequal numbers.

Complementary Studies

Five partitioning tests were run using shrimps of the same sex—two tests with males and three with females. Partitions allowing visual and chemical contact were used.

Five other partitioning tests were run using shrimps from which both antennae and antennules had been ablated with a small scissors. Partitions allowing visual and chemical contact were used, and the separation interval prior to removal of the partitions was shortened to five days, so that molting, and hence regeneration of appendages, would not occur before the animals were mixed.

To test for the existence of a "fight" pheromone, water was exchanged between an aquarium in which shrimps had just been fighting and one in which a pair was established. Five such experiments were done to test the theory that a "fight" pheromone might induce fighting in an established pair.

RESULTS

General Considerations

FIXED MOTOR PATTERNS: In observing shrimps, the following fixed motor patterns were recognized and recorded. Those originally described by Stolen (1964) are marked with an asterisk, while those newly identified by the author are described below.

(1) Agonistic behavior—threat and agression: (a) chelipeds apart*, (b) rushing*, (c) grab*, (d) antennae entwined*, (e) raised body (the legs flexed so as to lift the shrimp's body higher than normal off the substratum),

(f) chela open (the jaws of each chela spread apart).[4]

(2) Agonistic behavior—appeasement and flight: (a) backswimming*, (b) chelipeds closed*, (c) crouch (the walking legs flexed so as to lower the shrimp's body closer than normal to the substratum), (d) chela closed (the jaws of each chela shut together).

(3) Courtship behavior: (a) cleaning*, (b) antennae entwined*, (c) chelipeds surround*, (d) dance (a raised body position is assumed with the chelipeds moderately apart from one another. The shrimp then moves rapidly back and forth from side to side. This action was shown by four different females and was immediately followed by approach and courtship behavior by a male).

(4) Feeding*
(5) Grooming*
(6) Walking*

PAIR OCCURENCE IN THE FIELD: The collecting data indicate that *Stenopus* usually occurs in pairs. Each of the 24 pairs collected consisted of one male and one female.

Furthermore, laboratory experiments indicate that all field pairs are of male-female composition. For example, as shown in Figure 1, when individuals of the same sex are mixed after partitioning, no courtship encounters occur, and the intensity and duration of agonistic encounters are initially high. Actually, agonistic behavior remains permanently high between mixed individuals of the same sex, the decline in agonistic encounters with time shown in Figure 1 reflecting the fact that in some experiments one animal had already been killed. Subsequent test situations showed that initial agonistic behavior does not remain high between equally sized *Stenopus* of opposite sex, but rather is extinguished quite rapidly and is followed by courtship behavior.

Effects of Experience on Pair Formation

UNFAMILIAR ENVIRONMENT: A comparison of Figures 2A and 2B reveals that previously

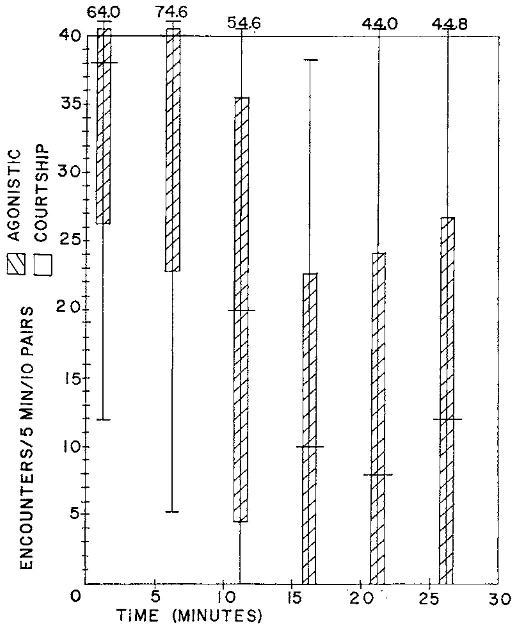

FIG. 1. Agonistic and courtship encounters when animals of the same sex are mixed, after partitioning allowing visual and olfactory contact. Encounters per 10 pairs calculated from 5 pair formation tests, involving a total of 10 animals. For each five minute interval the widest horizontal line indicates the mean number of agonistic encounters, a diagonally marked box indicates 4 standard errors of the mean (2 above and 2 below the mean), and the longest vertical line indicates 4 standard deviations (2 above and 2 below the mean). The relative distribution over each five-minute interval is not meant to be indicated for the respective behaviors, but only their totals per five-minute period.

unpaired *Stenopus* of opposite sex showed significantly more agonistic encounters if mixed without a preliminary partitioning interval (that is, in an aquarium with which they are unfamiliar) than they showed when mixed after a period of partitioning allowing no sensory contact (in an aquarium with which they are familiar) ($P > 99.5\%$, t test). In a separate situation, a pair which had been mixed for more than 2 weeks was observed to fight when moved to an unfamiliar aquarium. This was the only instance of fighting ever observed between an established pair. These observations indicated that the original control should be changed, and Experimental Situation I was replaced by Experimental Situation II.

[4] The two fixed motor patterns *chela open* and *chela closed* were included by Stolen in her behavior patterns *chelipeds apart* and *chelipeds closed,* respectively; however, cheliped movement and chela opening or closing can occur independently.

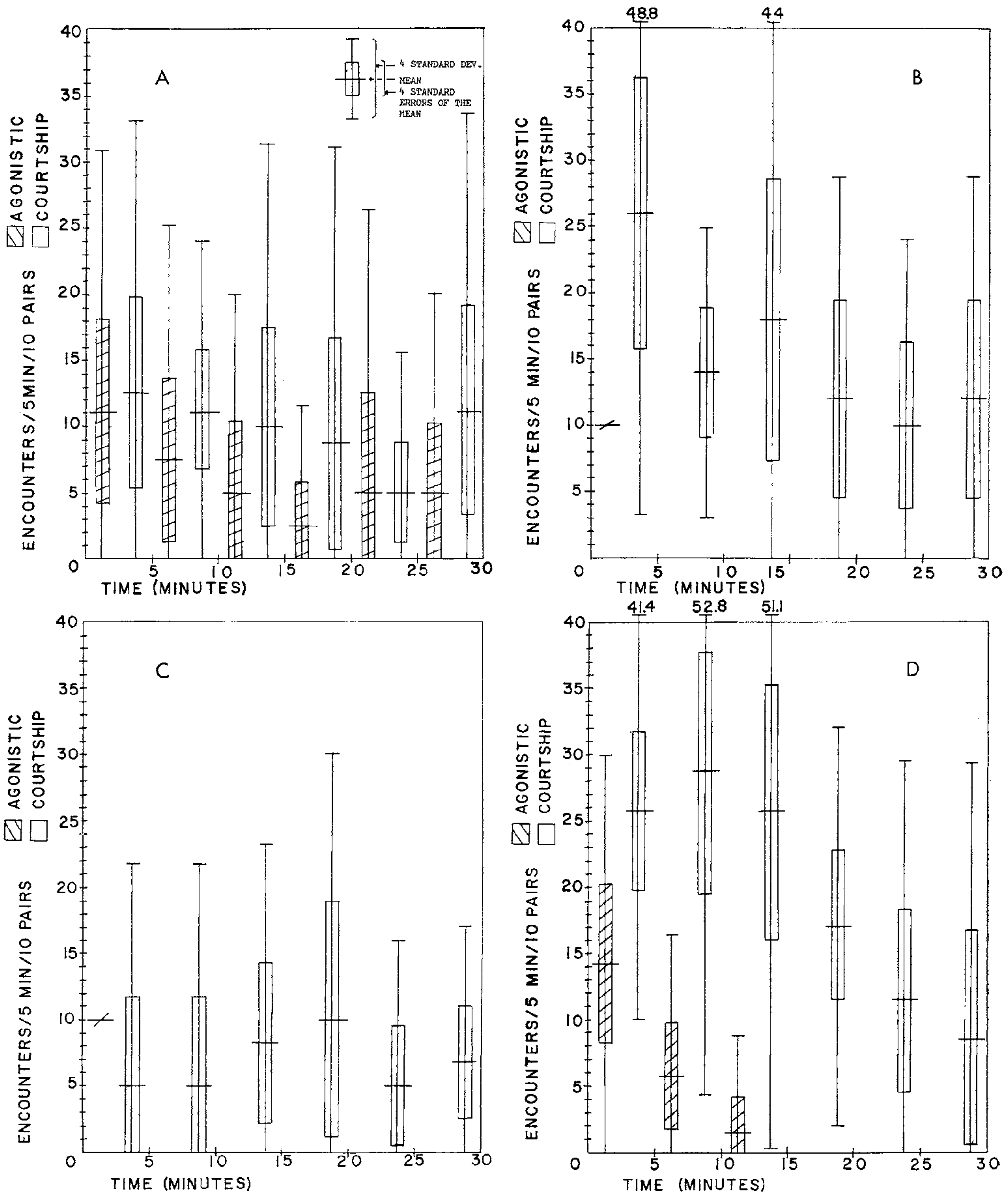

FIG. 2. Agonistic and courtship encounters when shrimps of opposite sex are mixed. *A,* With no partitioning interval allowed; encounters per 10 pairs calculated from 8 pair formation tests, involving a total of 15 shrimps. *B,* After partitioning allowing no sensory contact; encounters per 10 pairs calculated from 5 pair formation tests, involving a total of 10 shrimps. *C,* After partitioning allowing visual contact only; encounters per 10 pairs calculated from 6 pair formation tests, involving a total of 11 shrimps. *D,* After partitioning allowing olfactory contact only; encounters per 10 pairs calculated from 7 pair formation tests, involving a total of 14 shrimps.

(Note that in both Figures 2B an 2C agonistic encounters occur only in the first 5-minute interval, and are marked by a single horizontal line, the mean, with no apparent standard deviation or standard error. This is because there was exactly one agonistic encounter per pair prior to courtship, resulting in a standard deviation and standard error of zero.)

DEPRIVATION OF SENSORY CONTACT WITH OTHER SHRIMPS: Figure 2B shows that the number of both agonistic and courtship encounters tends to decrease with time, being higher in the first 5-minute interval than in any subsequent interval. This tendency shows that courtship motivation[5] is lowered with contact as the pair bond between shrimps is established. The experiment also suggests that the initial peak of courtship motivation is due to prior deprivation of physical and sensory contact with other shrimps. A series of experiments with regularly increasing deprivation intervals is needed to substantiate or refute the latter conclusion. Important for this paper is the comparison of this control situation with the subsequent experiments, since the comparative role of the various sensory modalities is the primary interest.

VISUAL CONTACT ONLY: In Figure 2C the courtship level during the first 5 minutes is significantly lower than that shown in Figure 2B ($P>99\%$, t test). The mean levels of courtship remain lower in Figure 2C throughout the 30 minutes, but the difference is not statistically significant. Thus, if prolonged visual contact alone is permitted during separation, subsequent courtship motivation reaches no initial peak. Agonistic encounters are at the same level in both experiments, indicating that prolonged visual contact has not altered agonistic motivation.

OLFACTORY CONTACT ONLY: In Figure 2D neither courtship nor agonistic encounters are shown to be significantly different from Figure 2B in the first 5 minutes; however, both behaviors are significantly higher in Figure 2D during the second 5 minutes ($P>99\%$, t test). The mean levels of courtship remain higher in Figure 2D throughout the 30 minutes, but the difference is not significant. Thus, prolonged olfactory contact strengthens both courtship and agonistic motivation.

VISUAL AND OLFACTORY CONTACT IN COMBINATION: Assuming that *Stenopus* responds equally to both visual and olfactory cues, one would suppose, judging from Figures 2B, 2C, and 2D, that in an experiment where both visual and olfactory contact were allowed (Fig. 3A), there would be a lower level of courtship than when only olfactory contact was allowed (Fig. 2D), and a higher level of courtship than when only visual contact was allowed (Fig. 2C). Experimental evidence supports the latter supposition, since courtship encounters are significantly more numerous in the first 5 minutes of Figure 3A than in the first 5 minutes of Figure 2C. Also, the mean levels of courtship remain higher in Figure 3A for the entire 30 minutes, although the difference is not statistically significant.

Experimental evidence does not, however, support the former supposition since, although courtship means are lower in the first 15 minutes of Figure 3A than in the corresponding period of Figure 2D, the difference is not statistically significant. Thus, when visual and olfactory cues are in combination, *Stenopus* responds primarily to olfaction.

TACTILE, VISUAL, AND OLFACTORY CONTACT: In Figure 3B, the number of courtship encounters is not significantly different from the number in Figure 3A; however, agonistic encounters are significantly fewer in Figure 3B ($P>99\%$, t test). Low agonistic behavior is more striking when individual tests are considered. There were no agonistic encounters in 7 of the 9 tests allowing tactile contact, and these were the only cases in all of the 65 tests performed in which no agonistic encounters occurred. The low agonistic behavior suggests that sex recognition occurred during partitioning, and hence that tactile contact facilitates such recognition.

[5] The term "motivation," as used in this paper, refers to all the factors which determine the tendency or probability that an animal will behave in a certain way. The term "motivational system" refers to the interaction of those internal and external factors underlying a specific category of behavior.

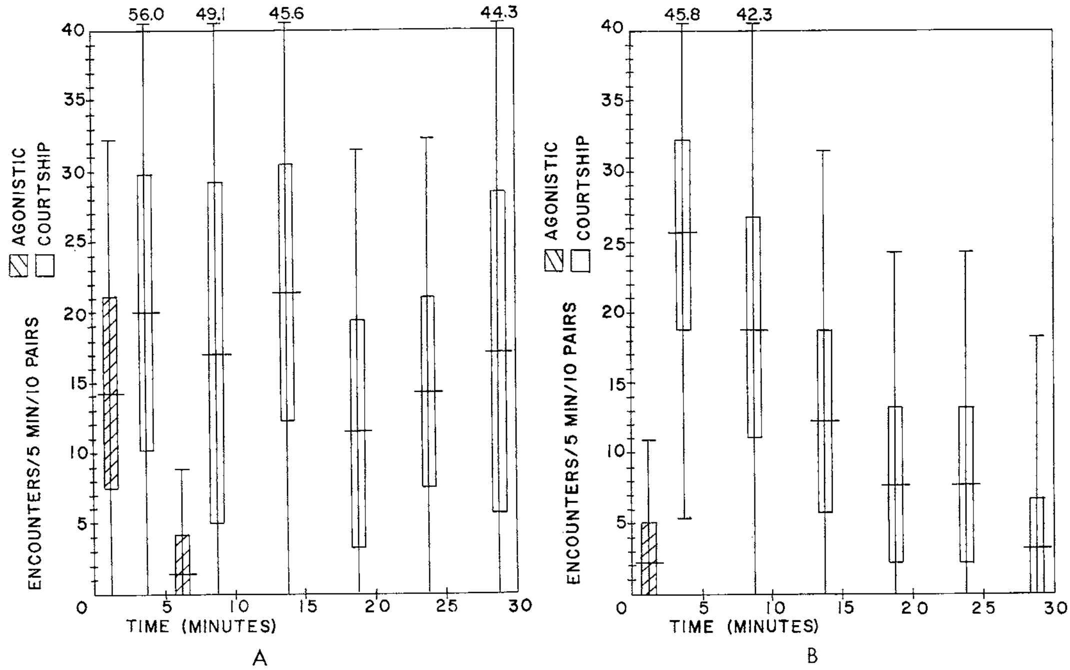

FIG. 3. *A*, Agonistic and courtship encounters when shrimps of opposite sex are mixed, after partitioning allowing visual and olfactory contact; encounters per 10 pairs calculated from 7 pair formation tests, involving a total of 14 shrimps. *B*, Agonistic and courtship encounters when shrimps of opposite sex are mixed, after partitioning allowing visual, olfactory, and tactile contact; encounters per 10 pairs calculated from 9 pair formation tests, involving a total of 16 shrimps.

Special Considerations

EFFECT OF SIZE DIFFERENCE ON AGONISTIC BEHAVIOR: A comparison of Figures 4A and 4B indicates that females tend to be aggressive toward smaller males. In Figure 4A agonistic encounters are significantly higher throughout the 30-minute interval, and courtship encounters are significantly lower throughout the first 15 minutes ($P>99\%$, t test). Thus, all experiments in which females exceeded males in size were disregarded in drawing Figures 1, 2, 3, and 5, and were treated separately.

EFFECT OF ABLATION: Ablation experiments (Fig. 5) to determine the importance of the antennae and antennules as locations for sensory receptors were inconclusive. It was hypothesized that, if touch receptors were located in these appendages, ablation of the appendages would prevent sex recognition; thus agonistic behavior would remain high. In three of the five tests, however, shrimps showed normal pairing, indicating touch receptors were located elsewhere on the body, or that another sense was substituted for touch. Shrimps without antennae and antennules showed increased visual responses, orienting toward the observer, rather than moving about their aquaria, and also assuming a threat posture when a hand was passed over or in front of the aquarium. Intact animals responded slightly or not at all to the observer or to the hand waving. The low levels of agonistic and courtship encounters during the first 10 minutes as shown in Figure 5, are due to lack of any movement by the shrimps. The high level of agonistic behavior after 10 minutes is due to two of the five tests. Although ablation of the antennae did not elucidate their role in pair formation, the behavior of the shrimps following ablation was apparently affected in some as yet unknown way.

PAIRING IN THE FIELD: Agonistic behavior between females and larger or equal-sized males is generally of short duration in aquaria. In 31 of 45 tests of such animals, involving a variety

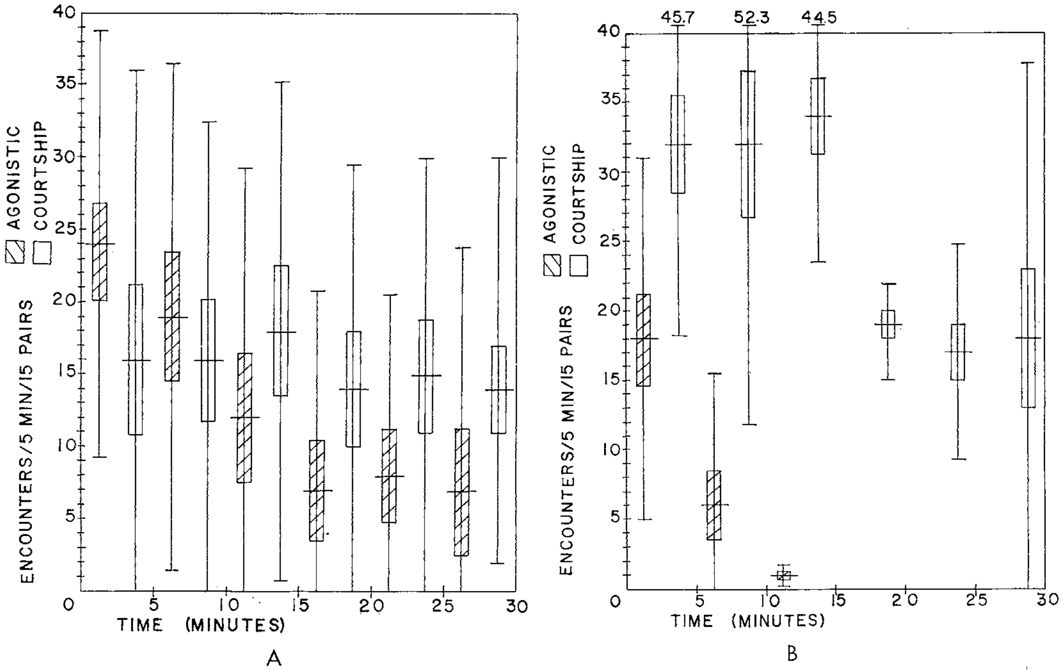

FIG. 4. *A*, Agonistic and courtship encounters when animals of opposite sex with females larger in size than males are mixed; results based on 15 pair formation tests, involving a total of 21 animals and a variety of partitions. *B*, Agonistic and courtship encounters when animals of opposite sex with males larger than, or equal in size to, females are mixed; results based on 15 pair formation tests, involving a total of 23 animals and a variety of partitions.

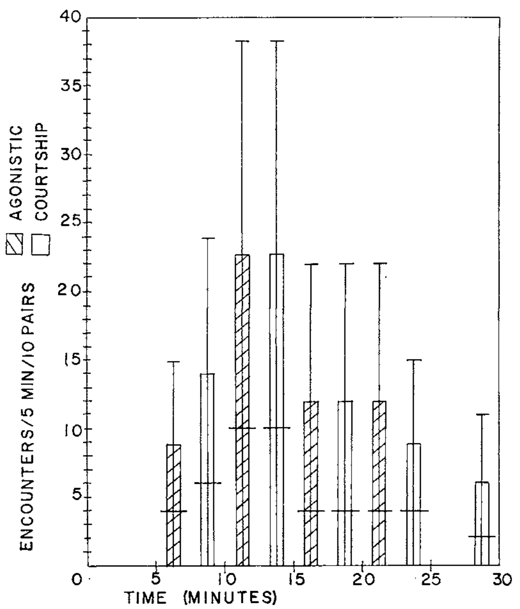

FIG. 5. Agonistic and courtship encounters when animals of opposite sex, with their antennae and antennules ablated, are mixed, after partitioning allowing visual and olfactory contact; encounters per 10 pairs calculated from 5 pair formation tests, involving a total of 5 animals.

of partitions, there was one agonistic encounter or less prior to courtship. This would indicate that field pairing probably occurs quite readily.

"FIGHT" PHEROMONE EXISTENCE: In these tests water exchange rather than shrimp exchange was undertaken to avoid the complicating variable of a new environment. No fighting was induced by water exchange in any of the five tests, indicating that either a fight pheromone was not present, or the experiments could not detect one.

DISCUSSION

There are numerous reports in the literature of behavior patterns in other Crustacea similar to those identified in *Stenopus*. In a review, Reese (1964) noted that behavior patterns such as threat postures and displays, ceremonial or ritualized fighting, submissive postures, and dominance hierarchies are quite common in marine decapods. For example, Crane (1958) observed threat postures in the fiddler crab, *Uca maracoani,* in which the crab stands higher on its pereiopods while the chelipeds are held in different attitudes, depending on the intensity of display. *Helice crassa* and *Hemiplax hirtipes* also show threat postures in which the former stands high on its pereiopods, and the latter extends its pereiopods laterally, and Beer (1959) suggested that the functional purpose of such postures in these two species of crabs is to make the individuals appear as large as possible. Shöne and Schöne (1963) reported the widespread existence of behavioral displays in crabs, mentioning that in *Ocypode* a raised body position of one individual causes a submissive, lowered body posture in another.

The reactions of *Stenopus* both to intraspecific size differences and to an unfamiliar environment are supported in the literature. Stolen (1964) found that large female *Stenopus* are very aggressive toward smaller males, and Reese (1964) concluded from the literature that larger marine decapods generally dominate smaller ones. Marler and Hamilton (1966) reported that novelty in the form of a stimulus, either qualitatively or quantitatively unusual, may cause approach or withdrawal in animals. It is possible that an unfamiliar environment makes one *Stenopus* individual more likely to respond agonistically toward another.

The functional roles of the various sensory modalities in pair formation provide an interesting system in which to study the relationships between stimuli, response, and feedback control of behavior in encounters between *Stenopus* individuals. Individual *Stenopus* can detect one another by visual, olfactory, and tactile senses. Olfactory contact strengthens a rise in courtship and agonistic motivation, visual contact inhibits the motivational rise, and tactile contact lowers agonistic motivation, presumably by sex recognition. Vision is of minor importance when in combination with olfaction. Based on these observations, Figure 6 shows diagrammatically the organization of pair formation behavior in *Stenopus.*

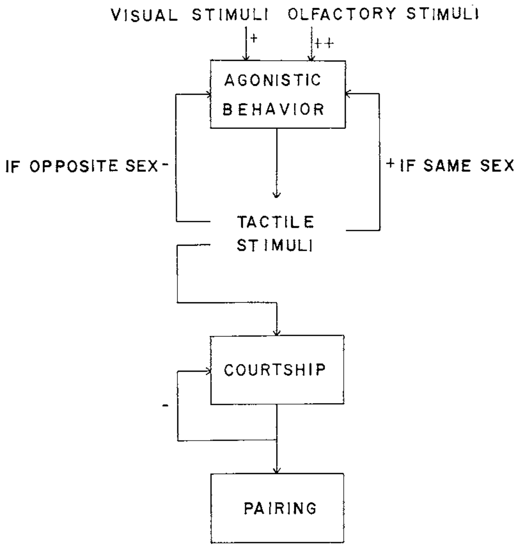

FIG. 6. Diagram of relationships between stimuli and feedback control of behavior in an encounter between two "stranger" *Stenopus* individuals.

Initial orientation toward another shrimp is by distance chemoreception, or by vision. These factors are believed to be relatively unspecific, thus releasing agonistic behavior. Stimulation of both these receptors prior to pairing would raise motivation for both courtship and agonistic behavior. Agonistic behavior results in tactile contact. Sex recognition and the subsequent decrease of agonistic motivation results from this contact. Tactile contact prior to pairing facilitates sex recognition, thus decreasing agonistic motivation. Vision is less effective, and thus would elicit significant response only in the absence of olfactive or tactile stimulation.

Sonic communication was not investigated because suitable testing equipment was not available. Sound communication in *Stenopus* seems unlikely, since no behavior indicative of sound production is evident, nor does *Stenopus* have any morphological features related to sound production. The presence of sharp, hooked projections over most of the exoskeleton makes any sort of rubbing seem unlikely.

The possibility that *Stenopus* may release and respond to pheromones should not be disregarded. Ryan (1966) demonstrated response to a female sex-attracting pheromone by male crabs of the species *Portunus sanguinolentus,* and both Hazlett (1966) and Kruschwitz (1967) demonstrated the existence of an "aggregating" pheromone in the hermit crab *Calcinus tibicen* and the shrimp *Saron marmoratus*, respectively. The effects of olfactory contact in *Stenopus* do not indicate that a pheromone originates in one sex or the other; however, further experiments are necessary to definitely eliminate this possibility. There is also no evidence for a "fight" or "fright" pheromone in *Stenopus*.

CONCLUSIONS

1. In the field, *Stenopus* is found in pairs, each pair consisting of a male and a female.
2. In aquaria, two *Stenopus* of the same sex show a high level of intra-specific agonistic behavior.
3. In aquaria, previously unpaired *Stenopus* of opposite sex show a short period of agonistic behavior followed by courtship, providing the male is equal in size to or larger than the female.
4. In aquaria, female *Stenopus* show a higher than normal level of agonistic behavior when the male is smaller.
5. *Stenopus* individuals may respond to one another by vision, olfaction, or touch.
6. Two previously unpaired *Stenopus* of opposite sex, separated with no opportunity for physical or sensory contact and then paired, show a high initial level of courtship which decreases with time (i.e., contact).
7. Visual contact during preliminary separation prevents an initial peak in courtship behavior.
8. Olfactory contact during preliminary separation strengthens the initial peak in both courtship and agonistic behavior.
9. When combined, olfaction plays a greater role than does vision in affecting courtship and agonistic behavior.
10. The addition of touch to olfaction and vision lowers agonistic motivation, which suggests that *Stenopus* identifies members of the opposite sex by touch.
11. *Chela open* and *raised body* are fixed motor patterns associated with threat and attack behavior.
12. *Chela closed* and *crouch* are fixed motor patterns associated with appeasement behavior.
13. *Dance* is a fixed motor pattern apparently associated with courtship behavior.
14. Introduction to a strange aquarium results in higher than normal levels of agonistic behavior.
15. A pheromone increasing the level of agonistic behavior or related to sex recognition was not demonstrated in *Stenopus*.

ACKNOWLEDGMENTS

I wish to express my deepest appreciation to Dr. Ernst S. Reese whose guidance, suggestions, and support were of major importance to the success of my research. I would also like to extend my sincere thanks to Lester Zukeron and Charles Nakamoto for their willing and conscientious assistance with my field work, to Lois Kruschwitz and Anne Rasa for their suggestions and aid in the laboratory, and to Lei Kihoi for her continual encouragement and motivational influence.

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